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(Received 3 Nov 1980; accepted 11 Feb 1981; revision received 2 Mar 1981.)

NOTES AND NEWS

VARIATION IN IMMATURE CONE COLOR OF PONDEROSA PINE (PINACEAE) IN NORTHERN CALIFORNIA AND SOUTHERN OREGON.—Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) has been the subject of much research, possibly as much or more than any other forest tree in North America. There are now more than 3500 articles that report on some feature or relationship of ponderosa pine; possibly one third of these deal exclusively with the tree (Axelton, USDA For. Ser. Res. Pap. INT-40. 1967; Gen. Tech. Rep. INT-12. 1974; Gen. Tech. Rep. INT-33. 1978). Yet only three of these make note

of immature cone color. For the cone color of 20 trees in Idaho, Maki (J. For. 38:55-60. 1940) reported 15 percent light (green to yellow-green), 50 percent dark (purple), and 35 percent medium (between green and purple). Krugman and Jenkinson (USDA Handb. 450. 1974) record vars. *arizonica* (Engelm.) Shaw and *scopulorum* Engelm. as green and var. *ponderosa* as green to yellow-green, rarely purple. Critchfield and Allenbaugh (Madroño 18:63-64. 1965) record only green-colored cones from the Sierra Nevada, but I observed trees with purple cones in northern California and southern Oregon. In 1976, in the South Warner Mountains of Modoc County, California, I noticed a decided increase in the frequency of purple cones with increased elevation.

A good crop on ponderosa pine in northern California and southern Oregon in 1978 provided the opportunity to study immature cone color more carefully. This was undertaken: (1) to test for correlations of cone color with other characteristics of ponderosa that vary in this region; (2) to determine whether cone color could be a marker for some economic criterion; (3) to understand better the relationship of ponderosa to other pines.

In 1978, cone color was recorded in mid-August for 33 locations (Fig. 1). Roadside positions that gave a view of a number of cone-bearing trees with front-lighting by the sun were selected. The crowns were scanned with binoculars and the cone color of each tree was classified into three categories. The color classification and nomenclature system of Kornerup and Wanscher was used (Politiken Forlag, Copenhagen. 1974) as follows—light (green to yellow-green, 28 and 29 A&B 6-8), medium (red to pale red, 8 and 9 B&C 6-8), dark (purple, 11 and 12 E&F 7-8). All cones on a tree were of one color class. Cones attacked by insects or that will abort are more nearly true pink and lack green pigment. Such cones are smaller and scattered throughout a tree among cones falling into one of the three basic classes. Any tree with cones not distinctly purple or green to yellow-green was placed in the intermediate category.

A series of viewing sites was used until 100 cone-bearing trees had been classified. This usually was accomplished in less than 1.5 km. At three sites only 50-75 trees could be viewed and classified easily because of the scattered location of cone-bearing trees. Each series was considered a plot. Though ponderosa pines have irregular cone crops, most trees in many locations had maturing cones in 1978; and it was assumed that the cone-bearing trees were representative of the area.

Each plot was placed into one of five groups on the basis of the frequency of trees in each of the three classes of cone color (Fig. 1). Virtually all trees in Group 1 plots had trees with only light-colored cones; less than 50 percent of the trees in Group 5 plots had light colored cones. Groups 2, 3, and 4 were gradations between 1 and 5.

The frequency of trees with medium and dark cones increased from south to northeast in the study area (Fig. 1). Group 1 and Group 2 plots were nearly all west of the Sierra Nevada-Cascade crest; Group 3, 4, and 5 plots were found only east of the crest.

Elevation may be associated with the shift in cone color in parts of the region. This possibility is shown best by the three plots in the South Warner Mts. at the headwaters of the Pit River (Fig. 1:A). The Group 3 plot there was at about 1800 m; the Group 4 plot at about 2100 m; and a Group 5 plot at about 2400 m. The next three plots along the Pit River (Fig. 1:B) reinforce the relationship of cone color to elevation. A Group 4 plot was at about 1500 m; two Group 3 plots to either side were between 1200 and 1500 m. Ponderosa pine is not abundant above 1800 m in this region, but I hypothesize that higher elevation stands generally will have higher frequencies of darker cones.

An elevational shift from green to purple was found by Sturgeon and Mitton (Amer. J. Bot. 67:1040-1045. 1980) for immature cones of white fir (*Abies concolor* [G. and G.] Lindl.) in southern Colorado. They reported only two colors, green and purple, and did not report geographical variation. They conclude that purple pigment functions in thermoregulation at high elevations.

Xylem monoterpene composition is associated with shift in cone color in that it changes abruptly in the general area of the study; 3-carene increased significantly while β -pinene, limonene, and α -pinene decreased significantly from south to north and east in northern California and southern Oregon (Smith, USDA Tech. Bull. 1532. 1977).

Sturgeon (Evolution 33:803-814. 1979), in an intensive study in the area, found the shift

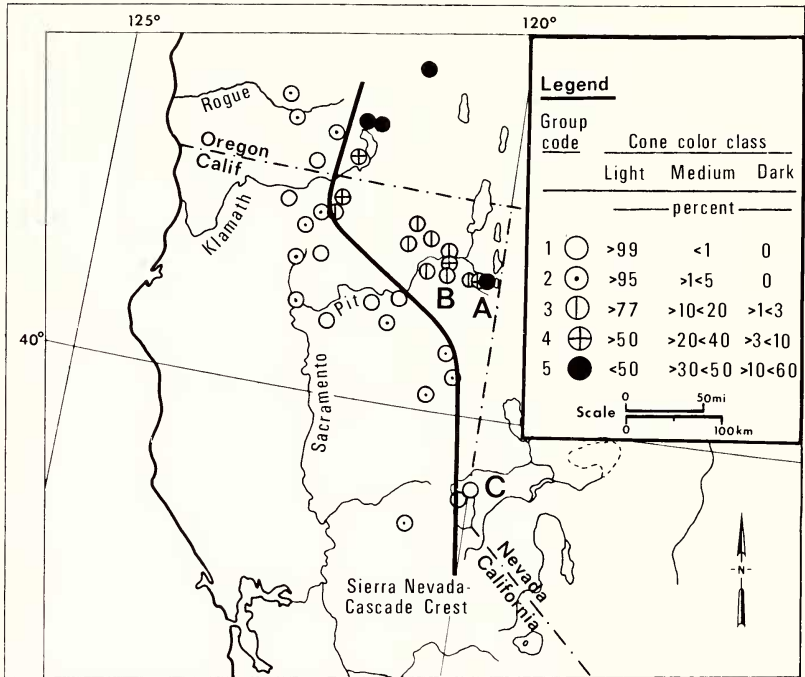


FIG. 1. Stand classification of ponderosa pine in northern California and southern Oregon for immature cone color. A. Three sites near headwaters. B. Three sites along the Pit River. C. Localized epidemic of mountain pine beetle in 1957-1959.

to occur generally at the Cascade Crest. Because data suggest that changes in resin composition are associated with cone color, three plots at the headwaters of the Pit River (Fig. 1:A) were analyzed for both characteristics simultaneously. The average monoterpene composition was essentially the same as that reported earlier (Smith, Madroño 21:26-32. 1971) but there was no consistent association with cone color. Trees with light-colored cones at the lowest elevation had the same approximate composition as trees with dark colored cones at the highest elevation and conversely. Resin composition and cone color appeared to be independent.

The susceptibility of ponderosa pine to the attack of the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) appears to shift in this same general region of California and Oregon. This insect historically has had a greater tendency to be epidemic in ponderosa pine east of the crest line (Miller, USDA For. Ser. File Rep. 1920; Eaton, J. For. 39:710-713. 1941). There have been no epidemics in ponderosa pine west of the crest line. This association probably does not imply causality because many variables other than monoterpene composition can influence the severity of bark beetle epidemics.

Speculations on the evolutionary relationships of ponderosa, particularly with Jeffrey pine (*P. jeffreyi* Grev. and Balf.) and Washoe pine (*P. washoensis* Mason and Stockwell), have been discussed by Haller (Madroño 16:126-132. 1961) and Wang (USDA For. Serv. Res. Pap. WO-24. 1977). Haller (1961) first concluded that Washoe pine arose through hybridization between Jeffrey pine and the Rocky Mountain variety of ponderosa pine (var. *scopulorum*). Later (Haller, Proc. Amer. Bot. Soc. 52:646. 1965), he suggested that Washoe pine arose from hybridization of var. *ponderosa* with var. *scopulorum*.

Both dark cone color and high proportions of 3-carene are characteristic of Washoe pine (Smith, 1971). I therefore conclude tentatively that at one time Washoe pine occupied many higher-elevation sites throughout northeastern California and southern Oregon. It has been replaced slowly by ponderosa pine. The process of hybridization between the two has produced ponderosa pines with dark- and medium-colored cones and with high 3-carene resin.

Color of immature cones may have more than one cause. It is possible that the hybridization of ponderosa and Washoe pine may have been the cause in northeastern California while having been selected for independently in southern Oregon. Sturgeon and Mitton's similar cone-color results with *Abies* (1980), however, suggest that dark-colored cones are somehow adaptive at higher elevations and may be selected for independently in different lineages. Haller's (1965) views of the ancient range and origin of Washoe pine are nevertheless consistent with the hybridization hypothesis.—RICHARD H. SMITH, Pacific Southwest Forest and Range Experiment Station, P.O. Box 245, Berkeley, CA 94701. (Received 17 Mar 1980; accepted 12 Jan 1981; final revision received 17 Feb 1981.)

REVIEWERS OF MANUSCRIPTS

Many people have contributed to the preparation of volume 28, in particular James C. Hickman, who served as associate editor during my initiation, and the editorial board members. Dr. Sterling Keeley, my colleague at the Natural History Museum in Los Angeles, has been particularly helpful. Reviewers of manuscripts are essential in maintaining the quality of any scientific journals, and the thoughtful, constructive criticisms of those listed below is gratefully acknowledged.

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